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THE DISSEMINATION OF FUNGI CAUSING DISEASE

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INTRODUCTION

A great deal has been written concerning the dissemination of seeds and this topic constitutes one of the regular subjects for treatment in every text book of elementary botany, but the dissemination of fungi is rarely mentioned. Even the text-books on fungi or plant diseases give but an inadequate account of this phase of mycology. Observations and experiments show that fungi provide for the dissemination of their offspring and the perpetuation of the species in many and varied ways and in many cases with great effectiveness. It is undoubtedly true that the agricultural and commercial practices of our present civilization have very materially assisted nature in spreading broadcast numerous parasitic forms as well as countless numbers of harmless saprophytes. That fungus pests are more numerous now in this country than in former years is not imaginary, but a stern reality. It is true that with the rapid development of plant pathology during the last decade we have had diseases of plants brought to our attention more than ever before. The history of our agriculture shows that with the intercourse between nations, fungus pests have been frequently transported from one country to another. It is my purpose to consider briefly some of the ways by which fungi, and especially those causing disease, have been and are being disseminated.

HOW FUNGI ARE CARRIED

In the first place brief reference may be made to the state in which fungi exist during their transport. They may be carried as spores, as sclerotia, or as mycelium. Most fungi produce from one to several different kinds of *spores*, or specialized reproductive bodies, which provide for the perpetuation of the species, just as seeds of our Spermatophytes provide for the production of more seed plants. Spores may be active, that is, motile or capable of locomotion, but in most cases they are not endowed with the power of movement; in the former case their own activity may carry them in an aqueous medium to points far away from the parent plant that produced them, but in the latter they must be transported by some outside agency.

Spores are produced by fungi in enormous numbers. It is undoubtedly true that vast numbers of spores perish without ever finding suitable conditions for the production of new plants. It has been estimated for some species of mushrooms that only one spore out of twenty billion ever produce a new plant capable of spore production.[1] Many contain a minimum of reserve food and become exhausted in their first attempt to establish themselves; some are not able to withstand adverse conditions, such as desiccation, low temperatures, etc.; certain types germinate at once without a resting period and thus frequently fail to reach a suitable substratum upon which to develop. Conidiospores may germinate at once and they are generally produced in much greater numbers than the more resistant ascospores which frequently require a resting period. Figures give but a slight conception of the enormous numbers of spores produced by fungi but they serve to emphasize their prodigality in spore production. It has been determined by careful analytic methods that a *small* "spore horn" or "tendril" of the chestnut blight fungus may contain as many as 115,000,000 pycnospores. Cobb states that a single head of smuted oats may contain as many as 500,000,000 spores, or a sufficient number to give 1000 per square foot if they were scattered evenly over an acre of ground. The marvel is that chestnut blight has not become more widely disseminated or oat smut a greater pest. Buller[1] estimates that a single wheat "berry" affected with bunt or stinking smut may contain over 12,000,000 spores; also that a single fruit body of *Polyporous squamosus* produced 11,000,000,000 spores, while the giant puff ball, *Lycoperdon boöista* L. produced the enormous number of 7,000,000,000,000 spores.

The production of *sclerotia*, or dense aggregates of fungus tissue by fungi is not uncommon, and these structures vary from minute masses to organs of appreciable size. Some fungi which produce spores but rarely, rely upon *sclerotia* for carrying the species over unfavorable conditions or for dissemination, while in other cases as in ergot, the sclerotium is only one stage in a rather complex life cycle. The origin of sclerotia is perhaps not uniform; they are probably due, in some cases, to the sterilization of a spore fruit, a pycnidium or perithecium, and certain fungi with scleropycnidia suggest this origin. Sclerotia appear to be very effective structures in perpetuating the species, if we may judge from the wide dissemination of certain fungi which are propagated almost entirely by this method. Why more fungi have not discarded the wasteful and uncertain process of spore propagation for the more certain method of sclerotia production can only be conjectured.

Fungi may be transported small or even great distances in the vegetative or *mycelial* stage. This mycelium may be included with some dead organic material which furnishes the substratum for its development or it may be included within the tissue of a plant or a plant structure upon which it is parasitic.

The following brief outline will give some of the principal ways in which the dissemination of fungi is effected:

- I. Seed-borne fungi—Seed dissemination.
  1. By true seeds or fruits.
  2. By vegetative reproductive structures.
- II. Air or wind-borne fungi—Wind dissemination.
  1. No explosive apparatus.
  2. Provided for by an explosive apparatus.
     - (a) Forcible ejection of the fungus spores from the fungus fruit.

III. Water-borne spores—Water dissemination.
   1. Active or motile spores.
   2. Passive or non-motile spores.
IV. Insect-borne fungi—Insect dissemination.
   1. Insects as carriers.
   2. Insects as hosts.
V. Dissemination by other animals.
VI. Dissemination by agricultural and commercial practices.
   1. Transport of soil or manure.
   2. Transport of infected seed, nursery stock, or hqst: cultural stock.
   3. Transport of various commodities.

SEED-BORNE PLANT DISEASES

Many fungi have certainly solved the problem of dissemination in a most effective way by a relation to the seed of the host plant at some point in their life history. The fungus may be carried in either the spore, sclerotium or mycelial stage, upon or within true seeds, fruits or vegetative reproductive structures such as tubers, roots, bulbs, etc. Many of these seed-borne fungi are pernicious pests and have attained as wide distribution as the hosts themselves. Since plant diseases have been more intensively studied, more and more illustrations of seed-borne fungi have been brought to our notice. Some seed-borne fungi appear so constantly and generally upon some of our common crop plants that the attendant symptoms are not unfrequently interpreted by the untrained, as a normal accompaniment.

Anthracnose of the bean was one of the first diseases that was demonstrated to be disseminated by true seeds. This was first proved by Frank[2] in 1883, although later investigations have repeatedly claimed the honor. The mycelium of the fungus grows through the pod and into the seed during the period of maturing, and is there ready to resume its growth when the seed germinates. Experiments tend to show that this disease is introduced into a field very largely if not entirely by the ruse of infected seed, and that the spores are not generally spread from one field to another by the wind.[3] The Ascochyta blight of peas is another disease that behaves in a similar way[4] and Barre has recently shown that the widely disseminated anthracnose of cotton bolls is of a like nature.[5]

Since infected seeds, in so many cases, show no external evidence of the disease, the fungus is insured a wide dissemination, even with the most careful practice in the selection of apparently clean seed. Seed-borne fungi do not appear to be confined to any definite groups but this method of dissemination may prevail whenever the ripening ovary is infected. The downy mildew of the Lima bean and the white rust of the oyster plant constitute two excellent illustrations from the Peronosporales. The seed of the oyster plant may be so badly infested with the white rust as to entirely destroy the crop. The black-leg or Phoma wilt of cabbage,[6] a disease known in this country only during the past few years, was undoubtedly introduced from Europe with imported seed. Chapman[7] has recently called attention to the seed dissemination of three different onion diseases: smut due to *Urocystis cepulae;* brown mold, caused by *Macrosporium porri;* and downy mildew, referred to *Peronospora schleideniana.*

Fruits which function as seeds may also act as carriers of the parasite. Perhaps the best known and most familiar illustrations of this class are the seed-borne smuts of cereals, in which case the fungus is either on the surface of the caryopsis in the spore stage or has penetrated the pericarp and persists as a dormant mycelium. The loose smut of oats and the stinking smuts or bunt of wheat are good illustrations of the former, while the loose smut of wheat is one of the most notable illustrations of the latter condition. The bunt or stinking smut of wheat is undoubtedly more prevalent in our cultivated wheat fields than any similar species upon a wild host, or at least it was until the introduction of fungus "steeps" for its prevention. The ordinary process of harvesting is one that has very materially assisted in the dissemination of the fungus. When a wheat plant becomes infected with bunt every head produced by a single stool is smutted and all the "berries" are destroyed or transformed into "smut berries." Smutted plants may be scattered here and there through the field, and during the threshing process smutted berries are mixed with the normal sound grain; but many of the smut grains have the thin outer membrane ruptured, thus setting free the spore mass and the individual spores become scattered over the normal grains, lodging particularly in the "brush" and in the suture.[8] Wheat may be so badly smutted that the normal grains are discolored by the large numbers of smut spores adhering to the berries. Of course nobody would think of using such grain for seed, but unfortunately smut spores may be present in minute quantity without giving any indication of their presence. It is possible, however, for the scientist to determine whether seed wheat is infected with bunt to even a slight extent. If the seed is washed or scrubbed in sterile water, the washings centrifuged, and the sediment examined with the microscope, the presence or absence of smut spores can be determined. This method was first used in this country by Bolley.[9]

In the loose smut of wheat wind dissemination of spores is combined with seed transport of the dormant mycelium. The inflorescence of wheat is completely destroyed and the dry, powdery mass of spores scattered by the wind. This maturity of the smut coincides nearly with the blossoming time of the normal head and the scattered spores may be responsible for a blossom infection. The fungus penetrates the developing ovaries and remains as a dormant mycelium hidden within the seed and exhibiting no warning of its presence. It is there, however, ready to resume activity with the awakening of the seed. Two diseases of beets are known to be carried by the seed (fruits): the Phoma rot of beets which has been so prevalent in Europe, and our well-known Cercospora leaf spot. The fungus (*Phoma betae*) which causes a rotting of the maturing beets also causes a serious damping-off of young seedlings.[10] A recent illustration has come to the writer's attention of chestnuts bearing the sclerotia of a fungus upon the surface.

Fungi which cause disease may be disseminated by the use of infected vegetative reproductive structures such as tubers, roots, rhizomes, bulbs or corms, for the production of a new crop. All such structures are gorged with reserve food and their tissues in a semi-dormant condition, easily invaded by certain types of fungi. In the majority of these structures the presence of an internal infection is revealed by some discoloration or disorganization of the storage tissue, or the fungus may be more superficial and exist in either the mycelial or the sclerotium stage. The Irish potato stands preeminent among the cultivated plants, for its numerous tuber-borne diseases. In recent years many of these tuber-borne diseases have made such headway as to seriously threaten the potato growing industry in many parts of the country. Mention may be made of the late blight of the potato with its internal mycelium, the dry rots which also produce internal discolored areas pervaded by mycelium, scab with the more superficial corroded areas, potato wart with its external warty excrescences, and Rhizoctonia or potato rosette with superficial sclerotia. It has been shown by Massee that wart may also be transported by the use of tubers which show no external evidence of the disease, the spores being lodged in the "eyes." Some of these tuber-borne fungi may so exist in the soil as to infect perfectly healthy seed, but their original introduction can be traced in numerous instances to the use of infected seed.

The sweet potato affords several illustrations of diseases which are frequently introduced by the use of infected seed roots. Among these may be mentioned the black rot, due to *Sphacronema fimbriatum*.[11] Several onion diseases may be introduced into new fields, by the use of infected sets or the use of imported bulbs for growing seed. Disease of the gladiolus are spread by the planting of corms already infected, and the same may be said concerning the bulbs of various greenhouse plants. As specific examples of bulb-borne diseases mention may be made of the Japanese lily disease, due to *Rhizopus necans,* and the anther smut of *Scilla latifolia* which develops from mycelium present in the bulb.

AIR OR WIND DISSEMINATION

The spores of many fungi are carried away from the parent plant by means of air currents. In general it may be stated that spores which are adapted to wind dissemination are liberated from the fungous fruit as a dry, powdery mass or are born singly or in loosely connected chains upon the ends of aerial sporophores, from which they are easily detached. The minute size of fungous spores makes unnecessary special devices for rendering them buoyant, and it is always possible to obtain various forms from the dust that settles to the surface of objects in closed rooms or in the garden or fields. The majority of the air-borne spores appear to be those of harmless saprophytic forms, and many of the statements made concerning the part which wind plays in the dissemination of parasitic species are based largely on analogy rather than supported by direct experimental evidence.

Observational evidence is of little value in determining the part of air transport of fungus pests which are confined to a single host, but some heteroecious rusts give us *undoubted* examples of wind dissemination which so far as I know have never been definitely proved experimentally. The cedar rust which alternates between the cedar tree and the apple tree, and must pass from one to the other, is an excellent example. Susceptible varieties of apples standing adjacent to infected cedars will show a high percentage of infection, sometimes as many as 200-300 distinct spots to each leaf and the number of infections per leaf will decrease with the distance until the average is either one or less to each leaf. In addition, the rapidity and universality of the infection following the gelatinous stage of the cedar apple can be explained in no other way than by the wind dissemination of the sporidia, which Coons[12] has shown are forcibly discharged from the promycelia. The part which wind plays in the spread of our cereal rusts has probably been greatly overestimated. The old idea that rusts are spread gradually by the wind from the southern plains country to the north as the season progresses, has been largely abandoned as our ideas of their life habits have been modified. The theory of the wind dissemination of the cereal rusts gives a beautiful example of the inefficiency of reasoning alone as applied to the processes of nature.

It is undoubtedly true that many of our present day statements in regard to wind dissemination of spores would need revision if the rigid test of experimental evidence were applied to them. The application of scientific methods to the determination of the part which wind plays in the dissemination of parasitic fungi opens up an interesting field for investigation. It may not be amiss to mention briefly some of the methods which may be utilized, and it may be stated at the beginning that these have already yielded valuable results in the few cases where tried.

In the employment of the *exposure plate* in the field under natural conditions the pathologist is but imitating the bacteriologist.

As far as I have been able to determine this method was first employed in this country in the field for determining the prevalence of parasitic fungi by Wolf[13] at the writer's laboratory in 1907. It had, however, previously been used by Saito in Japan. It should be emphasized in this connection that the exposure plates should be made under natural conditions if we are to obtain reliable results. Erroneous conclusions may be drawn from results obtained under artificial conditions even if they are obtained from field experiments. It is evident that this method is of value only when the spores of the pathogens under investigation will germinate upon the medium that is available. There are many parasitic forms the spores of which will not germinate upon the ordinary culture media, and in investigating the prevalence of these spores this method is clearly at fault. Exposure plates may be made in the field or in the laboratory with the substitution of an artificial air current. As an illustration of this type, the experiments of Fulton[14] with the spore horns of the chestnut blight fungus may be mentioned, although his negative conclusions would have been obtained by *a priori* reasoning.

It is at once evident that the exposure plate can give no exact quantitative results, but only the relative abundance of the forms obtained. The aspiration of the air through a "spore trap" and the determination of the number of spores per unit quantity of air can be readily performed by the employment of the ordinary bacteriological method. This method was used by Wolf in 1907 and has recently been employed by Anderson.[15] The poured plates in this method do not reveal the possible presence of spores which will not germinate upon our culture media. In order to determine the presence of these, other methods must be employed. There are two methods suggested which are somewhat comparable to the two just outlined. First, if quantitative results are not desired a glass funnel, the inner surface of which is coated with glycerine, may be exposed for a certain length of time in the open and the spores which fall into it washed down with sterile water and the washings centrifuged, after which the sediment thrown down may be examined with the microscope. If quantitative results are desired the aspirator should be used, the contents of the sugar tube dissolved in a known volume of sterile water, all or a unit quantity centrifuged and the sediment examined microscopically by the use of the Leitz-Wetzlar counting apparatus. The results of the microscopic tests may be substantiated by inoculations made by using a suspension of the spores obtained from the air analyses, and in certain cases this method can be used to good advantage.

Inoculations by wind-borne spores under controlled conditions has been used in some cases for determining the part which this method of transport of spores plays in the life history of the fungus. As an illustration, the inoculations with chestnut blight fungus made by Anderson may be cited. The wounds were protected so as to exclude insects and spores washed down the tree by rains.

A large number of fungi, the spores of which are disseminated by air currents, produce the spores in such a manner that they are easily detached and carried away by the wind or in a dry powdery mass. In such cases there is no explosive apparatus that ejects the spores into the air and it is entirely the force of air currents that sweep them away from some exposed position, or they are borne in such a manner that they rattle out of the fungous fruit, frequently as a result of agitation of the host plant by the wind.

In many fungi, particularly the ascomycetes and basidiomycetes, the spores are forcibly ejected into the air[1] and can then be swept away from the fruit by the wind. It should not, however, be concluded that all fungous spores that are forcibly ejected, are adapted for wind dissemination. There are numerous cases in which the forcibly ejected spores are not adapted for wind dissemination but after they have come to rest are removed to more distant locations by other agencies.

The loose smuts of cereals and other grasses which produce myriads of spores in the deformed or destroyed inflorescences of their hosts are supposed to be disseminated largely by wind-borne spores. The powdery condition of the spores, and their elevated position upon the host certainly suggests this method of transport. The uredospores and aecidiospores of many rusts and particularly the sporidia are wind-borne, while the summer spores of the powdery and downy mildews are produced in such a way as to suggest this method also. The aecial stage of *Gymnosporangium* *macropus* shows an interesting adaptation.[16] During dry weather the segments of the pseudoperidium are curved outward in stellate form but during humid or rainy periods they approach each other and partially or completely close over the spores. The spores are thus set free at a time when they are most likely to be carried away, and this is especially important in heteroecious forms which must reach the alternate host or fail to develop.

Judging from the results of experiments in the field it seems that the most prevalent spores belong to species of the imperfect fungi, and especially to the Hyphomycetes. Perhaps these facts are to be explained by the omnipresence of certain species of this group rather than to the fact that they are better adapted for wind dissemination. In the work carried out by Wolf only a single pycnidial form, Phyllosticta, was obtained during a long series of orchard tests. The work of Burrill and Barrett[17] on the wind dissemination of *Diplodia zeae,* the fungus causing dry rot of corn, may be mentioned in this connection. They found by field tests that spores of this fungus were carried by the wind and they attribute much of the infection to wind-borne spores from old stalks. There appears to be little direct experimental evidence to show to what extent ascomycetes which forcibly eject their spores from the asci are disseminated by the wind. In many cases the ejected spores are surrounded by a sticky material and *a priori* reasoning would suggest that in such cases they are not extensively carried by the wind. It is at least suggestive that the spores of ascomycetes are obtained so rarely in exposure plates in the open. Further investigations may show that ascospores are more generally scattered by the wind than present experiments show. It is the idea of the writer that wind-borne ascospores may be responsible for the spread of a fungus in the immediate environment, but that long jumps or wider dissemination are accomplished by other agencies than the wind.

The puffing of spores as in Peziza, Urnula, and other Discomycetes in which there is a simultaneous discharge of numerous asci, is undoubtedly an adaptation for wind dissemination. Since most of these fruits are produced close to the ground, the forcible expulsion of the spores must materially assist in their being carried away by air currents. In the Hymenomycetes the forcible expulsion of the basidiospores from the sterigmata helps simply in liberating the spores from the sporophores, while the normal position of the hymenium makes the fall of the spores inevitable, and convection currents assisted by wind carry them away to more distant points.

Spores that are destined for wind transport may be set free in a cloud by the explosion of the fruit of the host plant. A beautiful illustration of this is to be found in the smut infected fruits of Oxalis, which burst and liberate the spores in much the same way that the capsules of touch-me-not expel their seeds.

DISSEMINATION BY WATER

Liquid water plays a very important part in the dissemination of some disease fungi. In certain groups of fungi free water is necessary for the development of some stage in the life cycle, that is, in those that produce active or motile spores, swarm spores, or zoospores. These active spores make their way for a shorter or greater distance from their point of origin as a result of their own power of locomotion. In other cases passive or inactive spores may be washed down from the host plant by rains and carried away by natural water currents or spread along the course of irrigation ditches.

The aquatic habit has been retained to a greater or less extent by the various species of the pond scum parasites, the water-molds, the white rusts and the downy mildews. The parasites of the pond scums are completely dependent upon free water for their dissemination and this appears to be equally true of some Chytridiales parasitic on seed plants. The natural habitat of the cranberry is particularly favorable for the development of the cranberry gall due to *Synchytrium vaccini.* It is also noteworthy that *Urophlyctis alfalfae* has made its appearances in this country in a number of regions in the Pacific coast country where alfalfa is grown under irrigation.

The Saprolegniales or water-molds include a much larger number of saprophytes than parasites and in the majority of forms are strictly aquatic in habit. Some species are parasitic on the eggs and young of fish and also frequently gain entrance to the bodies of adults. While countless numbers of young fish and other aquatic forms annually fall a prey to the ravages of these fish molds, it is under the artificial conditions of the fish hatcheries, that the water molds are most likely to become epidemic. Not only may the water become filled with myriads of these motile spores of the water molds, but the diseased fish may transport the fungus for long distances and introduce it into entirely new localities.

There are two fungi which belong to the water molds that cause destructive plant diseases. One of these, *Pythium de Baryanum,* is the cause of a damping-off of seedlings, a great variety of species being attached. This fungus has attained practically a world-wide distribution. At just the periods that young seedlings are establishing themselves in the soil, this damping-off fungus finds conditions favorable for the development and dissemination of its swarm spores. These motile spores are able to swim actively in the soil water and are also spread by the spattering of rain and the meteoric water which flows over or through the surface layers of the soil. It is this production of enormous quantities of motile spores at times when the seedlings are young and susceptible that makes this one of the most destructive of the damping-off fungi. The other water mold referred to has been known to science only since 1906,[18] but when it first appeared in California it made such headway as seriously to threaten the citrus industries of that section of the country. The fungus in question, *Pythiacystis citrophthora,* causes the disease of lemons known as the brown rot, and the history of the discovery of the cause of this disease and of its method of dissemination forms one of the most interesting chapters in modern plant pathology. The natural habitat of the fungus is the damp soil of the orchard, and irrigation apparently favors its development. The spores of the fungus are not wind-borne and only fruit either in contact with the soil or very low down on the tree becomes infected. The motile spores can easily reach fruits in contact with the soil by swimming through the soil moisture, and the spattering of rain is supposed to carry spores to the lowermost fruits that are free from contact with the soil. If lemons were handled like apples in preparing them for the market, the brown rot would never have become such a serious pest, but lemons must be washed or scrubbed, and it is just this process that makes a more extensive infection possible. Dirt bearing the fungus is transported to the washer on the surface of the fruits and the fungus finds in the water of the washer favorable conditions for its development. The washers thus become infected with the fungus and the water through which the lemons must pass becomes filled with myriads of the motile spores, some of which may gain entrance to the fruit during the washing and scrubbing process. Of course greater care is now taken in cleaning the washers and the use of fungicides in the water prevents the development of the fungus.

The Peronosporales, including the downy mildews and white rusts are not so completely dependent upon moisture for the dissemination of the spores, since their conidia (sporangia) are borne in such a way as to be carried away by the wind. They do, however, show a greater dependence upon moisture than many of the fungi that have abandoned entirely the production of motile spores. It is an especially noteworthy fact that the late blight of the potato, caused by *Phytophthora infestans*, is epidemic during wet seasons and is limited geographically by rainfall. This partial dependence upon free water for its development probably explains the reason the late blight has never been a serious potato disease in the drier portion of the plains country.

It is undoubtedly true that rain and water currents play a very important part in the dissemination of fungus spores. In the first place rain may assist in the further transport of wind-borne spores that have been lodged upon plant surfaces. In case of wound infections the spores may be finally carried into the wound by rain washing down over spore laden surfaces, the spores finally coming to rest in a more favorable position for germination. Many fungus spores are rarely carried away from the fruits in which they develop except through the agency of rain. This seems to be particularly true of many forms producing pycnidia surrounded by a more or less evident mucilaginous secretion which prevents their release from the fruit or their separation from each other except in the presence of sufficient water to dissolve the cementing substances. Such spores may accumulate as sticky or waxy masses over the acervulus or they may be pushed out through the ostiole of a pycnidium as the result of growth of others within. In certain forms the extruded spore mass takes on the form of a long, coiled, flattened or cylindrical thread, which is designated as a "spore horn" or tendril. These sticky spores are produced in enormous quantities during warm, humid periods and the spore masses dry down and become hard if they are not washed away by rains. Many spores of this type retain their vitality for a considerable period as long as they are embedded in their mycelaginous secretion, but soon succumb to desiccation and other unfavorable factors as soon as they are separated by the rains.

In this connection several illustrations may be mentioned. *Valsa leucostoma,* the fungus causing die-back of peaches, plum and apricots produces conspicuous, brown or amber-colored tendrils which ooze out from the pycnidial stromata embedded in the bark. These are always abundant during the humid period following a rain, but disappear entirely except from especially protected positions during the first precipitation of any amount. During a warm rain the spores are being produced in enormous numbers but they are washed away as rapidly as they are extruded so the tendrils do not become visible until the rain has ceased. What has been said concerning the conidiospores of the die-back fungus applies equally well to those of the chestnut blight fungus, *Endothia parasitica.* It has recently been determined by experiments carried out under the writer's direction that the so-called summer spores are washed down from the blight lesions in enormous numbers, even during the winter rains when the temperature is but little above the freezing point.

There seems to be little evidence that the spores of bean anthracnose are wind-borne. The facts known concerning this disease indicate that rain and dew are of utmost importance in its spread after it has once been introduced by the use of infected seed. The fact that the spores of the Melanconiales are found so infrequently in the air lends support to the theory that these fungi are largely dependent upon rain and other agencies besides wind for their transport.

There is not much direct evidence to show the part of running water in the transport of non-motile spores. If these spores fall into streams or irrigation ditches there is every reason to suppose they will be transported for some distance. In some forms germination would take place in a few hours, and so the possibility of transport for long distances would be excluded. It is claimed that irrigation water plays a very important part in the dissemination of the late blight of celery in California.[19] The spores may be washed away from the pycnidia and carried along the trenches with the irrigation water.

INSECTS AND DISSEMINATION OF FUNGI

The relation of insects to the spread of plant disease is a subject to which sufficient attention has not been directed. The numerous insect-borne diseases of man and animals suggests a similar relation between insects and plant diseases. In most insect-borne animal diseases the insect acts as an intermediate host, and is not simply a carrier as is true in the case of the "typhoid fly." Not a single instance of an insect acting as an intermediate host for a fungus causing a plant disease has yet been brought to light, but the part which insects play in the dissemination of fungi is limited by their work as carriers and as producers of wounds which make infection possible.

It seems probable that insects play a very important part in the dissemination of saprophytic fungi. Fungus fruits are in many cases rich storehouses of food, and insects have become mycophagists, either utilizing the natural growths or becoming cultivators of fungi as is exemplified by the "ambrosia" beetles, or the ants with their fungus gardens. In visits to fungus fruits insects cannot fail to carry away spores, in much the same way that insects carry away pollen (spores) from the flowers which they visit. In some cases there seems to be a definite adaptation to insect transport of spores, while in others the transport is apparently only accidental.

The carrion fungi, of which *Phallus impudicans* may be taken as an example, attract flies to their spore-producing surfaces by their characteristic odor. The greenish slime in which the spores are embedded also contains three sugars, levulose, dextrose, and another intermediate between dextrose and gum. These and the spores are greedily eaten by flies. Fulton[20] has shown that flies transport the spores in millions by the adherence of them to their feet and proboscides, and also that the spores will germinate after they have passed through the digestive canal of these insects.

The sphacelia stage of the ergot of rye and other grasses gives a beautiful example of insect dissemination. The ovaries become infected at flowering time by wind-borne ascospores and the production of conidia soon begins. This production of conidia is accompanied by the secretion of a sweet substance, the so-called honey dew, which is eagerly sought by insects. A rapid dissemination of the fungus is accomplished since the visiting insects carry away spores and scatter them as they fly from flower to flower. Although the sooty mold of the orange and other citrous fruits is not a definite parasite, it becomes a troublesome pest. This fungus is associated with and spread by the white fly, or Aleyrodes and other species of aphid-like insects.[21] The secretions of sweetish fluid constitutes the pabulum which makes possible the development of the fungus. Some anther-inhabiting fungi are undoubtedly disseminated by insects. This is true of the smut of various species of the pink family. The affected anthers produce smut spores instead of pollen and these are carried from plant to plant by the visiting insects, thus assisting in the dispersal of the fungus.

The manner of spread of fire blight of the pear and apple was for many years more or less of a mystery. The bacteria causing the disease are set free upon the surface of the diseased parts in sticky droplets, and are quickly killed by exposure to sunlight and desiccation. Waite[22] first showed that the rapid spread of the disease during the spring is due to insects and especially to bees. The bacillus lives over winter in only a small percentage of the affected branches and is spread from these by insects. The blossoms become infected, the bacteria multiplying in the nectar, and thus the disease is spread from flower to flower by bees. Insects like leaf hoppers and others which bite the delicate young shoots are also important agents in the spread of fire blight.

An intimate relation between certain mites and the bud rot of carnations was established by the writer.[23] The mites are always found in the buds that have been rotted by *Sporotrichum poae;* they find in the mass of rotted petals a most favorable substratum for their development. The young mites which migrate from diseased to healthy buds carry spores of the fungus with them and thus inoculate the healthy buds, their presence serving to accentuate the severity of the trouble.

The literature of plant pathology contains not infrequent reference to the part which insects play in the dissemination of plant diseases, but these are in many cases generalizations not based on direct experimental evidence. Murrill and others[24] have stated that the spores of the chestnut blight fungus are carried by insects, but up to the present date there are no published experiments which really substantiate this statement. It seems probable, however, that this early claim will be supported by experiments now in progress.

Massee[25] has pointed out the fact that the rapid spread of apple canker due to *Nectria ditissima* in England coincides with the introduction and spread of the "American blight or wooly aphis." He makes the following statement: "I think it would be scarcely an exaggeration to say that if we had no "wooly blight" we should have no "canker," that is in the sense of an epidemic. It should be pointed out, however, that this opinion which is not based on experimental evidence is not entirely acceptable. The whole problem of the relation of insects to plant diseases is one that merits more attention than has been given to it, and investigations in this line may be expected to yield important results.

DISSEMINATION BY OTHER ANIMALS

The prevalent notion in regard to the part which other animals play in the dissemination of disease-producing fungi is expressed by the following quotations:

"Insects, birds, snails and slugs are known to be unconscious agents in the dispersion of spores, whereas dogs, hares, rabbits, etc., running through a field of corn, potatoes or turnips act after the fashion of the wind by bringing into contact adjoining plants.[25]

"Mites, flies, birds, mice, etc., carry spores adhering to their bodies from one place to another; and probably are frequently the unconscious cause of a new infection or the rapid spread of an epidemic due to fungi."

While the above are generalized statements based on but little experimental evidence this possibility has been demonstrated in some cases. Massee reports that snails and slugs are instrumental in spreading powdery mildews. Slugs allowed to crawl over mildewed leaves and then over healthy leaves left behind spores which soon caused the appearance of mildew along their pathway.

Birds, especially woodpeckers, have been mentioned by various writers in connection with the dissemination of the chestnut blight fungus. While the few tests reported to date (15) were negative it seems reasonable to believe that bird transport is a possibility. Woodpeckers frequently visit the chestnut blight lesions in search of insect larvae, and it will be remarkable if they do not carry away blight spores upon their feathers, bill or feet. While the writer is not yet ready to make any positive statement in regard to the part which birds play in the spread of this pernicious disease of the chestnut, a pertinent fact may be mentioned. By the employment of careful analytic methods a single hairy woodpecker has been found to be carrying as many as twenty different kinds of fungus spores. Johnson has suggested the possibility that the bud-rot of cocoanut may be carried by turkey buzzards as well as by certain insects and reports some experiments which seem to lend support to his contention.[26]

In considering this subject observations on and experiments with saprophytic fungi may be mentioned. Voglino[27] has shown that slugs eat the sporophores of fleshy agarics, especially the hymenium, and that the spores begin to germinate in their intestines and afterwards continue to grow in the ground in which the slugs burrow. The subterranean ascus-bearing tubers of truffles are sought as food by rodents and the spores of these fungi are supposed to be dispersed by this means.

Herbivorous animals play a very important part in the dispersal of certain dung-inhabiting fungi. A considerable number of these dung inhabiting fungi expel their spores with considerable force from the fruiting body. If it were not for the grazing animals these spores would in most cases, be carried no farther than the force of their projection would take them for they are sticky and adhere to the surface of the objects upon which they light. Foliage with attached spores is eaten by grazing animals and the spores being able to pass through the intestines of the animal unharmed, find a suitable substratum for their development at some distant point. Among those forms which have developed this habit the following may be mentioned: Pleurage, Ascobolus and other black-knot allies which shoot their spores by the explosion of the ascus; and certain Hymenomycetes like Coprinus and allies.

DISSEMINATION BY AGRICULTURAL AND COMMERCIAL PRACTICES

Numerous instances of the transport of disease producing organisms by man as a result of agricultural and commercial practices are known. With the development of our agriculture and the intercourse between nations the part of man in the dissemination of plant diseases has become more pronounced. The possibility of the spread of diseases and insect pests from one region to another has long been known and states have endeavored to safeguard the agricultural and horticultural interests of the people by laws relating to inspection of nursery and other stock. From the standpoint of fungus diseases this inspection has not been as effective as might be desired for in the majority of states the inspectors have been entomologists, familiar only with the more evident plant diseases such as crown-gall or black-knot, and not skilled in the detection and diagnosis of the more obscure troubles. This statement is not imaginary but is based on facts, for the writer has, in numerous instances, visited nurseries immediately after the official inspection and found various fungus diseases prevalent that were entirely overlooked. The demand for national legislation making restrictions which might govern the introduction of pests from foreign countries and the spread of troubles from infected regions to those free from the disease led to the recent passage of the Plant Quarantine Act.[28]

Fungi which are primarily soil dwellers may be carried by transport of soil. Spores which have not yet germinated may be incorporated with the soil but in some of the most serious troubles the fungus is present in the mycelial or in the sclerotial stage. One of the agricultural practices that should be condemned on this account is the use of alfalfa soil for the inoculation of a field with the nitrogen-fixing bacteria. If, for example, the soil selected contained the mycelium of the alfalfa Rhizoctonia or that of the southern fungus of cotton root rot, these troubles might be introduced into new fields. We have reason for believing that the sterile mycelium of such fungi will endure considerable dessication without losing its vitality. The "spawn" of mushroom growers is but mycelium preserved and temporarily dormant in dried bricks of compost. It is particularly in the cultivation of plants under glass that we find the introduction of fungi and other pests with the soil. The drop or Sclerotinia disease of lettuce is one that persists by the development of sclerotia that may remain in the soil.[29] It seems to be true that root-knot of roses is frequently introduced into greenhouses by the selection of soil previously infected with eel-worms.

Some parasitic fungi are capable of passing one stage in their life history in the soil or in compost. This is especially true in the case of certain smuts, of which corn smut is a most notable example. It is a common practice on farms to feed corn fodder or stover to cattle and return the compost to the soil. The smut spores find in the compost especially favorable conditions for germination and also for the production of secondary sporidia in countless numbers by a process of budding. Compost originating from the use of smut-infected corn may thus contain billions of sporidia of smut that are returned to the soil of the corn field where they are ready to produce new infections. The work of cultivation and the movement of wagons and teams from one field to another may be responsible for the spread of disease producing organisms. It is undoubtedly true that the mycelium of the cotton root rot is extensively spread through the fields during the cultivation of the crop. It is claimed by Massee that club root, or the finger and toe disease of cruciferous plants, may be spread by soil adhering to cart wheels, tools, shoes, etc. The practice of allowing diseased plants, fruits or other products to fall to the ground and remain there unmolested save for the work of nature's scavengers is a too common practice that favors the spread of disease.

The part which man has played and is playing today in the dissemination of plant diseases can not be overlooked. This is the inevitable result of our specialized agriculture and modern commercial practices, but the distribution of diseases by the importation of infected seed, nursery and horticultural stock, and the transport of various commodities, can and should be reduced to a minimum by the employment of all possible safeguards.

Many of our serious plant diseases have been brought to this country from Europe or other foreign countries, and we can point in turn to pests which have been transported from America to Europe and elsewhere. The influence of climatic and edaphic factors upon the development of disease in epidemic form must be taken into consideration. It is by no means certain that a fungus pest which has proved serious in one country will prove equally serious in another, but the existence of serious diseases in a country or region should be kept in mind, and importations of susceptible stock made with extreme care.

Commercial concerns, state agricultural experiment stations and departments of agriculture, and the United States Department of Agriculture are all importing seeds and plants from foreign countries, in the endeavor to find plants valuable for the trade or better suited to the agriculture of the country. If we reflect upon the nature of seed-borne fungi it must at once be evident that this wholesale importation of seed is bound to be a prolific source of the spread of disease. It is undoubtedly true that the black-leg of cabbage previously referred to was brought to this country by infected seed[6] and that potato wart recently reported from Newfoundland was introduced from England.[30] These are illustrations of recent importations and it was the discovery of this latter disease in this country that gave one of the strong arguments for the passage of the recent Plant Quarantine Act.

The shipment of nursery stock is frequently responsible for the appearance of diseases in hitherto uninfected territory. In the greater percentage of even well managed nurseries plant diseases of various kinds may be found in profusion, the massing together of individuals favoring their development, but the neglected nursery is literally a pest house of plant diseases. The Pennsylvania Chestnut Tree Blight Commission has records of spot infections of blight that were traced to the planting of nursery stock that was diseased at the time of shipment. The diseases of nursery stock that are accompanied by easily recognized symptoms, may easily be guarded against by rigid inspection of all stock offered for shipment, and fumigation is a reasonable safeguard against the spread of many insect pests, but unfortunately some of the most serious diseases can be carried by stock which shows no indication whatever of its presence. One of the most striking examples of this is to be found in the case of the seedlings of white pine affected with the so-called blister rust.[31] The fungus causing this trouble has a period of incubation in the bark of nearly a year before it causes the characteristic hypertrophies, and for this reason inspection at the time of importation is but an imperfect insurance against its introduction. In such extreme cases the quarantine of infected regions and the restrictions of shipment of stock that might carry the disease is entirely justifiable. Diseases like the black-knot, peach leaf curl, orange rust of raspberries and blackberries, and many others that produce a perennial mycelium in the host may easily be transported by infected nursery stock, while there are many opportunities for the transport of resistant spores on the surface of florists' greenhouse stock or field-grown plants. Besides this, incipient infections of various fungi may be present in either herbaceous or woody plants, and entirely escape detection at the time of shipment.

The transport of various commodities such as hay, grain, packing material, fruits, vegetables, wood, lumber and any crude plant products must play a part in the spread of plant disease. With our diversified trade relations with foreign countries and the extensive trans-continental shipments of plant products from west to east and from south to north, opportunities for the transport of plant diseases over wide ranges of territory are greater than ever before in entire progress of our agriculture.

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